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for **bnlg1014 (locus)**

This locus is also known by the following names:

bmc1014**bnlg1014****Type:** Probed Site**Species:** Zea mays ssp. mays**Linkage Group:** 1**Arm:** S (short arm)**Map Coordinates:** (* indicates the locus is on the backbone)

Map	Coordinate	Bin
A632/rtcs1 1999	20.00	1.01
bins 1	1.01	1.01
BNL 2002 1	41.68	1.01
Chromatin IBM 2003 1 *	62.80	1.01
IBM IDP +MMP bd (ver 4) 1	48.91	1.01
IBM neighbors v.2 1 *	76.40	1.01
IBM1 1 *	76.40	1.01
IBM2 1 *	82.80	1.01
IBM2 2004 neighbors 1 *	82.80	1.01
IBM2 2004 neighbors frame 1 *	82.80	1.01
IBM2 FPC0402 genetic neighbors 1 *	63.02	1.01
IBM2 neighbors 1 *	82.80	1.01
IBM2 neighbors frame 1 *	82.80	1.01
LHRF Gnp2004 1 *	16.00	
Pioneer composite 1999 1	20.70	1.01
SSR Consensus 1	24.50	1.01
SSR IBM 1 *	66.10	1.01
SSR Tx303xCO159 2002 1 *	21.90	1.01
SSR Tx303xCO159 2003 1 *	22.00	1.01

SSRs

p-bnl1014 (via SSR PCR)

Primers and Enzymes:**Primer/Enzyme**

CACGCTGTTTCAGACAGGAA

CGCCTGTGATTGCACTACAC

Probe

p-bnl1014

p-bnl1014

**Anchored BACs:** (BACs identified to be anchored by probes for this locus):

b0074A07

b0092D02

b0138L14

b0008N23

b0036L14

b0182A10

b0284B14

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An evaluation of the utility of SSR loci as molecular markers in maize (*Zea mays* L.): comparisons with data from RFLPS and pedigree

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Abstract The utility of 131 simple sequence repeat (SSR) loci to characterize and identify maize inbred lines, validate pedigree, and show associations among inbred lines was evaluated using a set of 58 inbred lines and four hybrids. Thirteen sets of inbred parent-progeny triplet pedigrees together with four hybrids and their parental lines were used to quantify incidences of scoring that departed from expectations based upon simple Mendelian inheritance. Results were compared to those obtained using 80 restriction fragment length polymorphism (RFLP) probes. Over all inbred triplets, 2.2% of SSRs and 3.6% of RFLP loci resulted in profiles that were scored as having segregated in a non-Mendelian fashion. Polymorphic index content (PIC, a measure of discrimination ability) values ranged from 0.06 to 0.91 for SSRs and from 0.10 to 0.84 for RFLPs. Mean values for PIC for SSRs and RFLPs were similar, approximately 0.62. However, PIC values for nine SSRs exceeded the maximum PIC for RFLPs. Di-repeats gave the highest mean PIC scores for SSRs but this class of repeats can result in "stutter" bands that complicate accurate genotyping. Associations among inbreds were similar for SSR and RFLP data,

closely approximating expectations from known pedigrees. SSR technology presents the potential advantages of reliability, reproducibility, discrimination, standardization and cost effectiveness over RFLPs. SSR profiles can be readily interpreted in terms of alleles at mapped loci across a broad range of maize germ plasm. Consequently, SSRs represent the optimum approach for the identification and pedigree validation of maize genotypes compared to other currently available methods.

Key words Simple sequence repeat · Microsatellite · SSRs · Maize · Variety identification

Introduction

Microsatellites, or simple sequence repeats (SSRs) are short nucleotide sequences, usually from 2 to 3 bases(b) in length that are repeated in tandem arrays. Amplifiable polymorphisms are revealed because of differences in the numbers of tandem repeats that lie between sequences that are otherwise conserved for each locus. Microsatellite loci have proven to be highly polymorphic and useful as genetic markers in many plant species including *Arabidopsis* (Depeiges et al. 1995), bur oak (Dow et al. 1995), maize (Senior and Heun 1993), seashore paspalum (Liu et al. 1995), rapeseed (Kresovich et al. 1995; Charters et al. 1996), soybean (Akkaya et al. 1992, 1995; Rongwen et al. 1995), sugar beet (Mörchen et al. 1996), sweet potato (Jarret and Bowen 1994) and wheat (Plaschke et al. 1995; Roder et al. 1995).

In this paper, we report the usefulness of SSRs as genetic markers to discriminate between, and to show associations among, inbred lines of maize using a greater number of loci and a broader diversity of maize germ plasm than has been reported previously (Senior and Heun 1993).

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Table 1 List and pedigree background of inbred lines used in the present SSR and RFLP profiling study

A632	Pedigree background ^a
A632	BSSS ^b C0 (94%), Minnesota 13 ^c (6%)
B73	BSSS ^b (100%)
Mol17	Lancaster Sure Crop ^c (50%), Krag ^c (50%)
PH207	Iodent ^c (59%), Long Ear ^c (20%), Minnesota 13 ^c (11%), Troyer Reid ^c (5%)
H64	BSSS ^b C0 (87.5%), Maiz Amargo ^c (12.5%)
PH595	Midland Yellow Dent ^c (2.5%), Southern U.S. Landrace Synthetic (19%), Funks G4949 (12.5%), Illinois Long Ear ^c (12.5%), Illinois Two Ear (12.5%)
PH642	BSSS ^b C0 (87.5%), Iodent ^c (9%)
PH814	Lancaster Low Breakage (25%), Southern U.S. Landrace Synthetic (19%), Osterland Yellow Dent ^c (16%), Funks G4949 (13%), Midland Yellow Dent ^c (6%), Tuson B ^d (6%), Brookings 86 ^c (5%)
PH848	Minnesota 13 ^c (12.5%), Osterland Yellow Dent ^c (12.5%), SRS303 ^c (12.5%), Iodent ^c (12%), Reid Yellow Dent ^c (12%), Lancaster Sure Crop ^c (6%), Longfellow Flint ^c (6%), MHW ^d (6%)
PHB09	BSSS ^b C0 (62.5%), Minnesota 13 ^c (25%)
PHB46	BSSS ^b C0 (50%), Alberta Flint ^c (25%), Osterland Yellow Dent ^c (25%)
PHB47	BSSS ^b C0 (87.5%), Brookings 86 ^c (12.5%)
PHB76	Smith TC ^d (25%), Midland Yellow Dent ^c (12.5%), NW Dent ^d (12.5%), Southern U.S. Landrace Synthetic (9%), Minnesota 13 ^c (8%), Funks G4949 (6%), Illinois Long Ear (6%), Illinois Two Ear ^c (6%), Osterland Yellow Dent ^c (6%)
PHB89	Coker 616 (25%), Lancaster Sure Crop ^c (12.5%), Midland Yellow Dent ^c (12.5%), Southern U.S. Landrace Synthetic (9%), Minnesota 13 ^c (8%), Funks G4949 (6%), Funks Yellow Dent ^c (6%), Illinois Long Ear ^c (6%), Illinois Two Ear (6%)
PHBE2	Iodent ^c (18%), Southern U.S. Landrace Synthetic (9%), Minnesota 13 ^c (9%), Osterland Yellow Dent ^c (6%), Midland Yellow Dent ^c (6%), Long Ear (6%), Funks G4949 (6%), Lancaster Low Breakage (5%)
PHBG4	Iodent ^c (27%), Minnesota 13 ^c (11%), Long Ear (9%), Coker 616 (8%), Midland Yellow Dent ^c (6%), Lancaster Sure Crop ^c (6%), Southern U.S. Landrace Synthetic (6%)
PHG12	BSSS ^b C0 (37.5%), Lancaster Low Breakage (25%), M3204 ^d (25%)
PHG29	Iodent ^c (59%), Long Ear (20%), Minnesota 13 ^c (13%), Troyer Reid ^c (5%)
PHG31	Iodent ^c (44%), Long Ear (15%), Minnesota 13 ^c (11%), Midland Yellow Dent ^c (6%), Southern U.S. Landrace Synthetic (5%)
PHG35	Iodent ^c (29%), Midland Yellow Dent ^c (13%), Minnesota 13 ^c (11%), Southern U.S. Landrace Synthetic (9%), Long Ear (9%), Funks G4949 (6%), Illinois Long Ear (6%), Illinois Two Ear (6%)
PHG39	BSSS ^b C0 (69%), Maiz Amargo ^c (25%)
PHG42	Iodent ^c (30%), Lancaster Low Breakage (10%), Southern U.S. Landrace Synthetic (9%), Osterland Yellow Dent ^c (9%), Minnesota 13 ^c (7%), Funks G4949 (6%)
PHG45	Iodent ^c (59%), Long Ear (20%), Minnesota 13 ^c (13%), Troyer Reid ^c (5%)
PHG50	Iodent ^c (35%), Long Ear (12%), Minnesota 13 ^c (12%), Osterland Yellow Dent ^c (7%), SRS 303 ^c (6%), Reid ^c (6%)
PHG53	BSSS ^b C0 (91%), Maiz Amargo ^c (6%)
PHG55	PROCOM ^b (50%), Minnesota 13 ^c (6%), Osterland Yellow Dent ^c (6%), SRS 303 ^c (6%), Iodent ^c (6%), Reid ^c (6%)
PHG69	BASS ^b (50%), BSSS ^b (50%), BSSS ^b C0 (25%), Alberta Flint (13%), Osterland Yellow Dent ^c (13%)
PHG71	BSSS ^b C0 (47%), Iodent ^c (30%), Long Ear (10%), Minnesota 13 ^c (9%)
PHG74	BSSS ^b C0 (89%), Minnesota 13 ^c (5%)
PHG80	Dockendorf 101 ^c (50%), BSSS ^b C0 (38%)
PHG81	BSSS ^b (50%), Iodent ^c (30%), Long Ear (10%), Minnesota 13 ^c (6%)
PHG83	Iodent ^c (30%), Lancaster Low Breakage (13%), Long Ear (10%), Southern U.S. Landrace Synthetic (9%), Osterland Yellow Dent ^c (9%), Minnesota 13 ^c (7%), Funks G 4949 (6%)
PHG84	Midland Yellow Dent ^c (13%), Southern U.S. Landrace Synthetic (9%), Minnesota 13 ^c (8%), Funks G4949 (6%), Illinois Low Ear (6%), Illinois Two Ear (6%), Osterland Yellow Dent ^c (6%), SRS 303 ^c (6%), Iodent ^c (6%), Reid ^c (6%)
PHG86	BSSS ^b (50%), BSSS ^b C0 (44%), Maiz Amargo ^c (6%)
PHJ76	BSSS ^b (50%), BSSS ^b C0 (38%)
PHK29	BSSS ^b C0 (63%), BSSS ^b (25%), Brookings 86 ^c (6%)
PHK42	Iodent ^c (59%), Long Ear (20%), Minnesota 13 ^c (13%), Troyer Reid ^c (5%)
PHMK0	BSSS ^b C0 (38%), Southern U.S. Landrace Synthetic (21%), BSSS ^b (13%), Dockendorf 101 ^c (13%)
PHMM9	BSSS ^b C0 (53%), Dockendorf 101 ^c (25%), Maiz Amargo ^c (13%)
PHN46	Southern U.S. Landrace Synthetic (12%), Iodent ^c (10%), Lancaster Low Breakage (9%), Osterland Yellow Dent ^c (9%), Funks G4949 (8%), Minnesota 13 ^c (6%), Midland Yellow Dent ^c (6%)
PHN65	BSSS ^b (50%), Minnesota 13 ^c (6%), Osterland Yellow Dent ^c (6%), SRS 303 ^c (6%), Iodent ^c (6%), Reid ^c (6%)
PHP38	BSSS ^b C0 (66%), Maiz Amargo ^c (13%), BSSS ^b (13%)
PHP85	BSSS ^b C0 (48%), BSSS ^b (38%), Maiz Amargo ^c (6%)
PHPE5	Iodent ^c (22%), Southern U.S. Landrace Synthetic (9%), Midland Yellow Dent ^c (9%), Minnesota 13 ^c (8%), Long Ear (8%), Coker 616 (6%), Funks G4949 (6%), Illinois Long Ear (5%), Illinois Two Ear (5%)
PHR03	Iodent ^c (25%), Minnesota 13 ^c (11%), Long Ear (8%), Southern U.S. Landrace Synthetic (6%), Midland Yellow Dent ^c (6%), Lancaster Sure Crop ^c (6%)
PHR63	Iodent ^c (29%), Coker 616 (13%), Minnesota 13 ^c (10%), Long Ear (10%), Lancaster Sure Crop ^c (6%), Midland Yellow Dent ^c (6%), Southern U.S. Landrace Synthetic (5%)
PHR92	BSSS ^b C0 (69%), Maiz Amargo ^c (25%)
PHT11	BSSS ^b C0 (47%), BSSS ^b (25%), Maiz Amargo ^c (13%), Alberta Flint (6%), Osterland Yellow Dent ^c (6%)
PHU55	BSSS ^b C0 (69%), Maiz Amargo ^c (25%)
PHV25	Iodent ^c (30%), Midland Yellow Dent ^c (13%), Long Ear (10%), Southern U.S. Landrace Synthetic (9%), Minnesota 13 ^c (7%), Funks G4949 (6%), Illinois Long Ear (6%), Illinois Two ear (6%)

Table 1 Continued

A632	Pedigree background ^a
PHV35	BSSS ^b (50%), BSSS ^b C0 (34%), Maiz Amargo ^c (13%)
PHV78	Iodent ^d (15%), Southern U.S. Landrace Synthetic (14%), Midland Yellow Dent ^e (13%), Funks G4949 (9%), Illinois Long Ear (6%), Illinois Two Ear (6%), Lancaster Low Breakage (6%), Long Ear (5%), Minnesota 13 ^f (5%), Tuson B ^g (5%)
PHV94	BSSS ^b C0 (53%), Dockendorf 101 ^h (25%), Maiz Amargo ^c (13%)
PHW52	BSSS ^b (50%), BSSS ^b C0 (34%), Maiz Amargo ^c (13%)
PHW53	Iodent ^d (21%), Osterland Yellow Dent ^e (11%), Minnesota 13 ^f (10%), Long Ear (7%), Lancaster Low Breakage (6%), SRS 303 ⁱ (6%), Reid ^j (6%), Southern U.S. Landrace Synthetic (5%)
PHWK9	Maiz Amargo ^c (50%), BSSS ^b C0 (50%)
PHZ38	BSSS ^b (50%), BSSS ^b C0 (41%)
PHZ51	Osterland Yellow Dent ^e (14%), Lancaster Low Breakage (13%), Southern U.S. Landrace Synthetic (9%), Minnesota 13 ^f (8%), Funks G4949 (6%), SRS 303 ⁱ (6%), Iodent ^d (6%), Reid ^j (6%)

^a Contributions of 5% or greater by pedigree are provided

^b Iowa Stiff Stalk Synthetic

^c Open-pollinated variety

^d Derived from Tuson, an open-pollinated variety from the West Indies

^e Population derived from Minnesota 13 open-pollinated variety

^f Stiff Root and Stalk or Stalk Rot Synthetic selection from Krug

^g Dawes open-pollinated variety from Nebraska most likely from Reid obtained from Mount Haleb, Wisconsin

^h Smith top-cross derived from HATO ding synthetic

ⁱ Northwest Dent, open-pollinated variety once grown in northwest and north central U.S.

^j Synthetic from Mississippi

^k Composite of Southern U.S. prolific germplasm and Corn Belt lines made by W. L. Brown in the 1960's; known as "BS11" at Iowa State University

^l Hybrid once sold by Dockendorf

Materials and methods

DNA was extracted from 58 maize inbred lines (Table 1) and from four maize hybrids (Pioneer hybrids 3183, 3377, 3732, and 3747). The 58 inbreds encompass a broad range of genetic diversity for Corn Belt materials, including pairs of lines that span pedigree relationships from unrelated to highly related. Among these inbred lines were 13 sets of triplets (a progeny line and both its parents) that provided opportunities for tests of inheritance and/or reliable band scoring. In addition, four hybrids were also profiled, providing additional opportunities to check the scoring and inheritance of polymorphisms. Initial DNA extractions were made using the CTAB procedure (Saghai-Maroof et al. 1984). Subsequent DNA extractions were performed using a proprietary method for which patent protection is being sought. Both methods provide DNA suitable for amplification by these SSRs and gave equivalent results. SSR loci were individually amplified using DNA of each inbred and hybrid using protocols described by Chin et al. (1996), except that fluorescent-labeled primers were used. Samples containing 0.5 µl of the PCR products, 0.5 µl of GENESCAN 500 internal lane standard labeled with N, N, N', N'-tetramethyl-6-carboxyfluorodamine (TAMARA) (Perkin Elmer-Applied Biosystems), and 50% formamide were heated at 92°C for 2 min, placed on ice, then loaded on 6% denaturing acrylamide gels. DNA samples were electrophoresed (29 W) for 7 h on an ABI Model 373A automatic DNA sequencer/fragment analyzer equipped with GENESCAN 672 software v. 1.2 (Perkin Elmer-Applied Biosystems). DNA fragments were sized automatically using the "local Southern" sizing algorithm (Elder and Southern 1987). PCR products from individual samples were assigned to specific alleles at each locus based on "binning" of a range of sizes (± 0.5 bp) as determined by ABI GeneScan™ and GENOTYPER™ software using the "local Southern" algorithm. Primer pairs for 200 potentially useful SSR loci were identified from the sequence data of maize that were published in Genbank, from di-repeat libraries made by Ben Burr (Brookhaven National Laboratory) and Lynn Senior (North Carolina State University), and from additional sequences available within Pioneer Hi-Bred Inter-

national, Inc. An initial screen of nine inbred lines was used to evaluate utility (Chin et al. 1996). Sequence data for primers to amplify these SSRs are available via the electronic maize database (Maize DB, Polacco 1996). Attempts were made to profile all of the 58 inbred lines and four hybrids with these SSRs. It was possible to obtain profiles for all of the inbreds and hybrids included in this survey for 131 SSRs (see Table 2). Genomic locations for most SSRs are provided according to the nomenclature used in Coe (1996). Among this set of SSRs, 59 (45%) were di-repeats, 36 (27%) were tri-repeats, 21 (16%) were tetra-repeats, 7 (5%) were penta-repeats, 5 (4%) were hexa-repeats, 2 (2%) were septa-repeats, and 1 (1%) was an octa-repeat.

RFLP data were obtained by Linkage Genetics (Salt Lake City, Utah) using DNA extraction and other protocols described by Helentjaris et al. (1985). Eighty single-locus probes that collectively sampled every chromosome arm were used.

PIC values were calculated using the algorithm:

$$PIC = 1 - \sum_{i=1}^n f_i^2 \quad i = 1, \dots, n$$

where f_i^2 is the frequency of the i^{th} allele.

PIC provides an estimate of the discriminatory power of a locus by taking into account, not only the number of alleles that are expressed, but also the relative frequencies of those alleles. PIC values range from 0 (monomorphic) to 1 (very highly discriminative, with many alleles in equal frequencies). For example, a marker locus that reveals five alleles, but where one allele is found in very high frequency (e.g., freq. = 0.9), has overall less discriminatory capability than a locus that also has five alleles, but in which those alleles are found in more equal frequencies.

Genetic distances between pairs of inbred lines from SSR and RFLP data were calculated from comparisons of the band scores using a modified Nei's distance (Nei and Li 1979). Pedigree distances between pairs of inbreds were calculated from 1-Malecot's Coefficient of relatedness (Malecot 1948). Associations among inbreds from SSR, RFLP and pedigree data were revealed using average linkage cluster analysis.

Results

SSRs that failed to amplify against the majority of inbreds or which gave amplified products that could not be clearly resolved were re-amplified and electrophoresed a second time. If results were still poor, then primers were re-designed (designated with '-2' following the SSR locus name) for further evaluation. If amplified products still failed to yield clearly scorable profiles for less than 95% of the inbred lines, then those SSRs were discarded from this study. This exercise resulted in scorable data being obtained for the 58 inbreds and four hybrids from 131 SSRs (Table 2). Primers with different sequences for loci already published (Coe 1996) may result in amplification products with different molecular weights from those obtained using the initial primer sequences.

Thirteen parent-progeny triplets were available for the examination of inheritance and scoring accuracy. For SSRs, non-Mendelian scores (where an amplified product was scored in a progeny inbred that had not been scored in one or both parental inbreds) ranged from 0 to 7 of the SSRs (0-5.3% of SSRs) per triplet. The mean was 2.85 incidences of non-Mendelian scoring (2.2% of all SSRs) per triplet. For RFLPs the range of non-Mendelian scores was from 0 to 7 RFLPs per triplet (0-8.8% of RFLPs per triplet). The mean for RFLPs was 2.85 (3.6% of RFLPs) incidences of non-Mendelian scoring per triplet.

Twenty five of the 131 SSRs were associated with one or more incidences of non-Mendelian scoring in the triplets. One SSR (bngl 619), a di-repeat, was so detected in four triplets; phi 011, a tri-repeat resulted in non-Mendelian scores for three triplets; six SSRs gave rise to non-Mendelian scores in each of two triplets; the remaining 17 SSRs that gave rise to non-Mendelian scores did so in only single triplets. Of all the SSRs implicated in non-Mendelian scoring, ten were di-repeats (16% of all di-repeats), eight were tri-repeats (24% of all tri-repeats), five were tetra-repeats (24% of all tetra-repeats), and two penta-repeats (33% of all penta-repeats).

Incidences of non-Mendelian scoring (absence of a parental band in a hybrid or presence of a non-parental band in a hybrid) expressed as a percentage of the 131 SSR loci for each hybrid were 3% for Pioneer brand hybrids 3183 and 3377 and 1.5% for Pioneer brand hybrids 3732 and 3747. The mean was 2.3% per triplet. Of the 12 instances of non-Mendelian scoring that were found, 11 were due to the absence of one of the inbred parental bands in the hybrid and one resulted from the presence of a band in the hybrid that was scored in neither parent.

PIC values for SSRs are presented in Table 3. PIC values for SSRs ranged from 0.06 to 0.91; the mean PIC for SSRs was 0.62. Summary data for numbers of bands

and PIC values for each repeat class are presented in Table 4. Di-repeats gave high PIC values (0.70). Other frequently used classes (tri- and tetra-repeats) resulted in PIC values of 0.53 and 0.59, respectively.

Associations among inbreds on the basis of pedigree, RFLP and SSR data are presented in Figs. 1, 2 and 3, respectively. Associations of inbreds on the basis of pedigree (Fig. 1) were similar to that which could be expected on the basis of either marker method (Figs. 2 and 3). Very similar associations of inbreds were revealed from analyses of the RFLP and the SSR data (Figs. 2 and 3). The correlations of pairwise distances

Table 2 a SSR markers and map locations; primer sequences are given by Coe (1996)

SSR Locus	Genomic Location	SSR Locus	Genomic Location
phi056	1.01	bngl249	6.01
phi097	1.01	bngl107	6.02
bngl182	1.03	bngl480	6.03
bngl439	1.03	phi031	6.03
phi001	1.04	bngl176	6.04
bngl421	1.05	phi070	6.06
bngl615	1.07	phi025	6.07
bngl100	1.08	phi078	6.07
phi011	1.10	phi057	7.01
phi055	1.10	phi112	7.01
phi094	1.10	phi114	7.02
bngl504	1.11	bngl657	7.03
phi064	1.11	bngl434	7.03
bngl108	2.04	bngl155	7.04
bngl166	2.04	phi082	7.06
bngl420	2.04	bngl669	8.03
phi083	2.04	phi115	8.03
bngl602	3.04	phi119	8.03
uc030	3.04	bngl240	8.04
phi029	3.04	phi014	8.05
phi073	3.05	phi060	8.05
bngl197	3.07	phi015	8.08
phi072	4.01	phi080	8.08
phi021	4.02	phi017	9.02
bngl490	4.04	phi028	9.02
bngl667	4.04	phi033	9.02
bngl252	4.05	phi044	9.02
phi096	4.05	bngl127	9.03
phi092	4.08	bngl244	9.03
phi093	4.08	bngl430	9.03
bngl589	4.10	phi022	9.03
phi006	4.10	phi027	9.03
phi019	4.10	phi061	9.03
phi076	4.10	phi065	9.03
phi024	5.00	phi016	9.04
bngl143	5.01	phi042	9.04
bngl105	5.02	bngl128	9.07
phi113	5.02	bngl619	9.07
phi008	5.03	phi059	10.02
bngl653	5.04	phi063	10.02
bngl278	5.06	bngl640	10.03
bngl609	5.06	phi071	10.04
phi085	5.06	phi084	10.04
bngl386	5.09	bngl236	10.06
bngl238	6.00	bngl594	10.06
phi075	6.00		